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The Energetic Cost of Feather Synthesis Is Proportional to Basal Metabolic Rate

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Abstract

The cost of feather production, C_f (kJ · [g dry feathers]$^{-1}$), differs substantially between species. We studied the molt cost in one insectivorous songbird (bluethroat, Luscinia s. svecica*) and one granivorous songbird (common redpoll,* Carduelis f. flammea*). We wanted to test whether differences in diet, body mass (or basal metabolic rate, BMR), or the latitude of molt could explain interspecific differences. In each individual, the resting metabolism, as measured by indirect calorimetry, was positively correlated with feather production rate. The cost of feather synthesis was estimated at 836 and 683 kJ · (g dry feathers)$^{-1}$ in the bluethroats and redpolls, respectively. The efficiency of feather production was 2.6% and 3.1%. It was concluded that neither diet nor latitudinal constraints alone could explain the differences found between species. The cost of feather production was significantly correlated with both body mass and mass-specific BMR, BMR_m (kJ · g^{-1} · d^{-1}), where BMR_m currently showed the highest degree of explanation, although other factors that influence BMR_m cannot be discounted. The C_f for a species with known BMR_m may be estimated from the equation $C_f = 270\ BMR_m$. Species with a relatively high BMR for their size also have a relatively high C_f. The tight association of C_f and BMR_m between species, and the low efficiency values of feather synthesis, suggests that feather production costs include more than the costs for keratin synthesis: they mainly consist of costs of maintaining tissues necessary for feather production.*

Introduction

The energy costs for a bird to renew its plumage involve the production of new feathers and increased thermoregulatory expenses due to higher ther-

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mal conductance (reviews by Payne [1972], Kendeigh, Dolnik, and Gavrilov [1977], King [1981], Murphy and King [1991, 1992]). While a general rise in energy metabolism during molt has been reported for a wide range of species (see, e.g., Payne 1972; King 1981; Croxall 1982), the cost of producing a given amount of feather mass has only rarely been measured.

For three small, mainly granivorous, passerine species, the house sparrow, *Passer domesticus*, the white-crowned sparrow, *Zonotrichia leucophrys*, and the chaffinch, *Fringilla coelebs* (body mass 20–30 g), feather production cost (C_f) has been estimated to be around 400 kJ · (g dry feathers)$^{-1}$ (Blackmore 1969; Chilgren 1975 (cited in King [1981]); Dolnik and Gavrilov 1979; Murphy and King 1984). In two larger carnivorous species, the long-eared owl, *Asio otus*, and the European kestrel, *Falco tinnunculus* (body mass 200–300 g), C_f was much lower, around 100 kJ · (g dry feathers)$^{-1}$ (Wijnandts 1984; Dietz, Daan, and Masman 1992). Dietz et al. (1992) hypothesized that this difference may be due to differences in either diet or size between the two groups.

Murphy and King (1984) showed that white-crowned sparrows do not need to increase their metabolizable energy intake (ME) solely to meet protein or specific essential amino acids (EAA) requirements for feather synthesis, as had been suggested by Dolnik and Gavrilov (1979). It is still possible, though, that the differences in C_f between the small seed eaters and the raptors may be related to their diets. For example, the efficiency of keratin synthesis could be higher in carnivorous birds (Dietz et al. 1992).

The energetic efficiency of feather production (5%–20%) is surprisingly low compared with the 40%–50% efficiency in the synthesis of other protein-containing tissues in animals (Reeds 1991). It has therefore been suggested that the rise in metabolic rates during molt does not reflect only the cost of formation of keratin as such. Energy may also be spent on production and maintenance of tissues needed for feather synthesis (King 1981; Murphy and King 1984, 1991; Dietz et al. 1992). Dietz et al. (1992) estimated that, if the cost of these (mainly unknown) physiological modifications vary in parallel to basal metabolic rates (BMRs), it would roughly explain the difference in C_f found between the passerines and the raptors.

Recently, Murphy and King (1990, 1991) proposed another explanation for the large variation found in C_f. They suggested that much energy is lost when birds store protein during the day for use in feather synthesis at later nonfeeding periods in the diel feeding cycle, for example, at night. The more protein has to be stored and transformed, the greater the loss would be. Feather production cost would therefore be inversely proportional to day length and thus to the latitude at which the birds normally molt (Murphy and King 1990, 1991).

To distinguish between the diet and the size (or BMR) hypotheses (Dietz et al. 1992), we compared the C_f's of two similar-sized species with different diets: the insectivorous ("carnivorous") bluethroat, *Luscinia s. svecica* (17 g) and the granivorous common redpoll, *Carduelis f. flammea* (13 g). As these species normally molt in continuous daylight or when nights are very short, we can also evaluate the latitude hypothesis of Murphy and King (1990, 1991). The size hypothesis would predict high molt costs for both species. The diet hypothesis would predict high values in the redpoll and lower values in the bluethroat. The latitude hypothesis, although not specifically addressed by our current experimental protocol, would predict that C_f's in bluethroats and redpolls are relatively low. The two new values of molt cost allow us to present a first allometric analysis of the association of molt cost with both body mass (m) and BMR.

Material and Methods

Birds and Housing Conditions

From May 26 to June 5, 1991, 24 bluethroats (all males) and 17 redpolls (both sexes) were trapped in mist nets near Ammarnäs, Swedish Lapland (65°58′ N, 16°07′ E), under license from the National Swedish Environmental Protection Board. The birds were brought by car to Lund, southern Sweden. From there they were flown to the Netherlands on June 10 and immediately brought by car to the Zoological Laboratory in Haren.

For other experimental purposes (effects of day length on molt performance), the birds were divided into two groups and kept under different light regimes. The birds on which the present article is based were all kept under a light regime (civil twilight) of 66° N latitude (i.e., Ammarnäs). That meant continuous light until August 1 and from then on nights of increasing length (night was 4 h and 39 min on August 15, 7 h and 17 min on September 1, and 11 h and 2 min on October 1). The birds were kept in separate cages ($40 \times 40 \times 40$ cm^3). Feeding activity was not recorded. Temperature was held constant at +15° ± 1°C to mimic natural conditions as closely as possible, and light intensity varied between cages from 120 to 720 lx.

As we wanted to estimate C_f both by indirect calorimetry and by food balance trials, we assigned six birds of each species to each of these two groups. As the average daily food intake actually decreased during molt in the bluethroats (5.4 ± 0.7 g [SD] dry food before molt and 5.1 ± 0.5 g during peak molt; paired t-test, $t = 1.69$, $P = 0.15$, $n = 6$) and did not increase to any significant degree in the redpolls (3.1 ± 0.4 g [SD] dry food before molt and 3.3 ± 0.5 g during peak molt; paired t-test, $t = 0.55$, $P = 0.62$, $n = 4$),

it proved impossible to estimate the C_f in this way (see King 1981). Accordingly, this article will only deal with C_f's as estimated from indirect calorimetry. The lack of increase in food intake during peak molt was probably due to reduced locomotory activity.

Bluethroats were fed (daily) ad lib. a mixture of boiled eggs (including shells), dry bread, ground calf hearts, commercial insect food, and vitamins and minerals, as well as 10–15 mealworms. The mixture contained 23.6 kJ · (g dry mass)$^{-1}$ and 29.0% crude protein. Redpolls received a mixture of different small seeds. The seed mixture contained 22.2 kJ · (g dry mass)$^{-1}$ and 14.4% crude protein. Birds were supplied with fresh water every second day, for drinking and bathing.

Molt Scoring

The birds were scored for molt every fifth day. The growth of flight feathers (primaries, secondaries, tertials, and tail feathers) was recorded according to the method of Ginn and Melville (1983). Old feathers score 0, growing feathers score 1–4 depending on their length, and 5 refers to a full-sized new feather. Scoring of wing feathers was only done on the left wing, but the right wing was regularly checked for possible asymmetry. A primary score (PS) was calculated for each molt scoring occasion by adding the score for the nine large primaries. Primary scores (for one wing) thus ranged from 0 (molt not yet started) to 45 (all primaries new). These PSs were used to assess the general progress of molt, enabling us to measure the birds in comparable stages. Molt duration was calculated as the time between the shedding of the first primary and the day when the waxy sheaths were no longer present at any feather.

All growing flight feathers were measured to the nearest millimeter. The body plumage and the wing coverts were divided into 13 feather tracts (table 1). On each scoring occasion, the percentage of feathers growing in each feather tract was estimated visually. In addition, the birds were weighed on a Pesola spring balance to the nearest 0.1 g. Their fat loads were scored from 0 to 8 with a modified version of the scale of Pettersson and Hasselquist (1985).

Field data on postnuptial molt have been collected on bluethroats and redpolls in the Ammarnäs area since 1983. Standardized trapping was carried out each year in the period July 12–August 20 (see Lindström 1987). Comparisons are made with this largely unpublished data set where appropriate.

TABLE 1

Average dry mass of feathers and feather growth duration for different feather tracts in the six bluethroats and five redpolls studied

Component	Bluethroats						Redpolls					
	Mass (mg)	SE	Range	Growth Duration (d · feathers^{-1})	SE	Range	Mass (mg)	SE	Range	Growth Duration (d · feathers^{-1})	SE	Range
Flight feathers:												
Tail	82	1.6	77–88				68	3.0	59–74			
Primaries	161	4.7	141–173				136	6.3	118–148			
Secondaries	67	1.4	61–71				49	1.2	45–52			
Tertials	22	.6	20–24				13	.3	12–14			
Body feathers:												
Great coverts	19	1.0	15–22	14.2	1.1	10–17	15	.8	13–18	12.4	1.0	10–15
Median coverts	84	1.9	77–89	13.7	.9	12–17	68	5.3	47–77	10.8	1.6	8–17
Primary coverts	15	1.2	12–21	13.0	1.3	8–15	12	.6	10–14	12.2	1.2	8–15
Throat	54	3.2	46–65	15.0	.9	12–18	38	3.3	32–50	16.8	1.0	13–18
Breast	240	7.8	204–262	16.3	.9	15–20	270	33.1	154–343	19.0	1.3	15–23
Flanks	103	6.5	79–121	13.8	.9	10–16	106	11.1	69–134	13.0	1.1	10–17

Under tail coverts	20	1.3	17–25	24.5	1.4	20–29	23	3.5	12–30	20.0	1.4	15–22
Legs	15	.5	14–17	13.0	1.5	10–19	16	1.9	9–19	13.6	2.0	8–18
Under wing coverts ...	34	2.7	24–44	14.5	1.1	11–17	33	1.3	29–36	11.0	1.3	9–16
Head	90	6.6	68–111	13.3	1.3	11–19	85	3.5	77–95	14.4	1.1	12–18
Back	128	6.1	112–153	15.2	1.0	11–18	139	17.4	76–183	17.2	1.1	13–19
Rump	40	4.2	26–57	13.8	.9	11–17	59	8.6	28–79	16.8	.8	14–18
Upper tail coverts	19	7.9	9–58	25.3	.8	22–28	10	.5	9–12	23.4	1.4	20–28
Total feathers	1,193	20.8	1,110–1,252				1,140	89.0	806–1,314			
Flight feathers	332	7.3	300–351				265	10.4	240–284			
Body feathers	861	23.5	773–925				875	81.7	567–1,033			
Body mass (g):												
Live	19.9	.6	17.4–21.2				16.0	.7	13.6–17.5			
Lean	16.7	.3	15.9–17.8				12.9	.4	11.8–14.1			
Lean dry	6.5	.3	5.6–7.5				5.2	.2	4.6–5.8			

Note. When estimating daily feather production rates for each individual, the individual values of feather mass and growth duration were used. Flight feather production was calculated with feather-specific values for each individual. In general, flight feathers grew with about 3 mm · d^{-1}. The average postmolt body compositions for the same birds are also presented.

Carcass Analysis

The birds were killed within a week of molt completion (most of the remaining birds of the other treatment groups were released). We plucked all feathers from the body and one wing. Feathers from the different tracts were kept apart and dried for at least 2 d at +60°C before weighing to the nearest 0.01 mg. To estimate fat and water contents the carcasses were dried at +60°C for at least 2 d and subsequently were boiled for 6–12 h in petroleum ether. They were then dried for 2 d and weighed again. We define lean mass as live weight minus extracted fat and lean dry mass as lean mass minus water.

Estimating Feather Production Rate

For each bird, the feather production rate (g dry feathers · d^{-1}) was estimated separately for body feathers (for convenience, the wing coverts are included in this group) and flight feathers.

Body Feathers. The feather growth duration (GD) was estimated, for each feather tract of each individual, as the number of days elapsing between the emergence and completion of the first growing feathers (table 1). The rate of production for each feather tract (g dry feathers · d^{-1}) at any given moment was estimated as the percentage of feathers growing times the dry feather mass divided by GD. When relating metabolic rate to feather production rate, we used data from the molt scoring session closest to the night of metabolic measurements. There was never more than 2 d between these two estimates.

Flight Feathers. For one bird of each species, the length (mm) and mass (to nearest 0.01 mg) of all individual flight feathers were measured. Mass was corrected for differences between individuals by using the individual values of overall primary mass, secondary mass, and so on, but assuming that the proportional distribution of mass among feathers was the same for all individuals. Feather mass was divided by feather length to estimate the mass · mm^{-1}. Each time metabolic heat production of a bird was measured (see below) we estimated how much different feathers had grown during that day. Feather production rate was assumed to be the same for night and day (Murphy and King 1986). Finally, we combined estimates of feather production rate of body and flight feathers to give the total feather production rate in g · d^{-1}.

Metabolic Measurements

Metabolic heat production was calculated from measurements of oxygen consumption in an open-circuit system. The birds were kept in metabolic chambers (1.4 L) that were placed in darkness in a temperature cabinet. Darkness was chosen as the experimental situation to avoid variation in activity level interfering with the assay of molt cost. Dried air was pressed through the system at a rate of 30 $L \cdot h^{-1}$, as measured with a mass flow controller (Brooks 5850TR) on the dried inlet air. The oxygen concentration of the outlet air was measured every minute (S3A, Applied Electronics), and the data were stored on an Olivetti PC. Oxygen consumption was corrected for the difference in volume of inlet and outlet air (Hill 1972). For the correction we assumed a respiratory quotient (RQ) of 0.75, resulting from oxidation of fat and protein. Therefore, we used an energetic equivalent of 19.8 $kJ \cdot L^{-1}$ oxygen consumed (Gessaman and Nagy 1988). For further details of the experimental design, see Dietz et al. (1992).

Before measurements, the birds had free access to water and food. Measurements started around 1900 hours local time, and the birds were returned to their cages around 0900 hours the next morning. We used the lowest 30-min average of the measurement period as an estimate of resting metabolic rate. The birds were weighed before and after each trial. The metabolic heat production was measured at +28°C, which was supposed to be within the thermoneutral zone (Gavrilov and Dolnik 1985). During the initial measurements, some of the bluethroats showed unreasonably high metabolic rates at this temperature, possibly because of heat stress. Therefore, bluethroats were subsequently measured at +20° and +24°C (within the same night, shifting at midnight). The measurements were taken before molt started (within 30 d) and within 14 d after molt completion, as well as three times during molt, at different molt intensities (PS 8–13, 26–34, and 44–45).

Statistics

For statistical evaluation of the results, we used one-way ANOVA, repeated-measures analysis (with the CONTRAST = DIFFERENCE option in the multivariate ANOVA [MANOVA] procedure) and ANCOVA, with SPSS/PC + V3.0.

Results

General Molt Performance

The bluethroats started to molt on average July 21 (SD = 4.1 d, range July 19–30, $n = 6$). This is similar to the onset of molt in the wild (17 male

bluethroats in PS 1–2 averaged July 19, SD = 2.7, range July 12–23; Å. Lindström et al., unpublished data). Molt progressed in the normal sequence, starting with the innermost primaries (cf. Haukioja 1971). Primary molt lasted 54 d (SD = 6.9 d, range 47–68, n = 6), whereas the full period of feather growth lasted 62 d (SD = 8.2, range 52–77, n = 6). At PS 44–45, the last molted secondaries were in their final stage of molt and very few body feathers were growing. The bluethroats produced on average 40 mg dry feathers · d^{-1} when molt was at its highest rate. All wing and body feathers were molted (table 1).

Body mass increased during the first part of molt, with a concomitant increase in fat score (fig. 1). During the second part of molt m decreased,

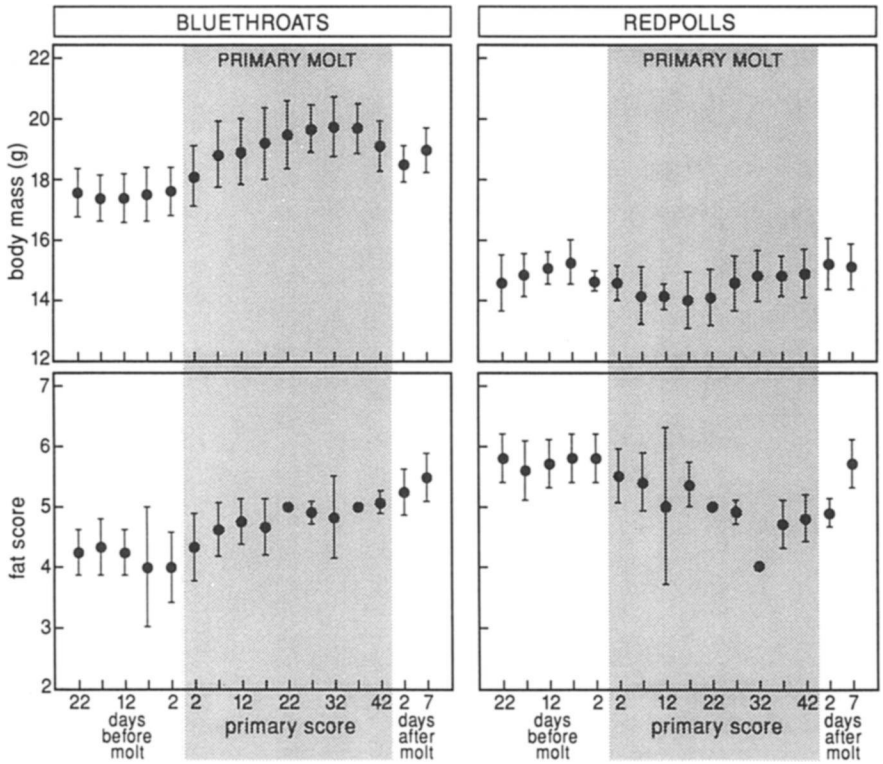

Fig. 1. Average body masses and fat scores (±SD) of six bluethroats (left) and five redpolls (right), before, during, and after molt. For the period of primary molt (hatched), which spans almost the complete period of molt, average values are given for periods spanning a primary score of 5. Since there were individual differences in the length of the molt period, the scale during molt is not completely proportional to time. Before and after primary molt, values are given for every 5 d.

whereas fat scores were stable. The completion of molt was accompanied by an increase in both m and fat scores.

In the redpolls, timing and speed of molt varied more than in the bluethroats. Molt started on average July 27 (SD = 6.1 d, range July 20–August 3, $n = 5$). Among wild birds in Ammarnäs, 72 birds with PS 1–2 were caught on average July 31 (SD = 7.7 d, range July 17–August 17; Å. Lindström et al., unpublished data). A sixth bird in the group did not start to molt until September 8. It arrested its molt after renewing the six inner primaries and some parts of the body plumage. This bird is left out of further analyses. In the remaining five birds, molt apparently progressed normally (Evans 1966; Newton 1969), and primary molt lasted 67 d (SD = 4.6, range 60–73). The complete molt lasted 87 d (SD = 10.9, range 69–100, $n = 5$). Redpolls with PS 44–45 were growing more feathers than bluethroats in the corresponding molt stage. Several secondaries were growing at their highest rates, and 10%–20% of the feathers in some body feather tracts were yet to be grown. During the most intensive phase of molt, the redpolls produced about 39 mg of feathers (dry mass) daily. The amount of feathers produced in each feather tract can be found in table 1.

In contrast to the bluethroats, m in the redpolls dropped slightly as molt progressed, reaching a low at PS 15–19. Fat scores decreased in parallel. From then on, m and fat scores increased slowly until the end of molt. As in the bluethroats, the end of molt was followed by rising m's and fat levels. The changes in m and fat levels during molt follow, for both species, the pattern found in wild birds at Ammarnäs (Å. Lindström et al., unpublished data).

Metabolic Rate

The premolt BMR in the bluethroats was on average 39.7 kJ · d^{-1} (SD = 9.1). During peak molt intensity, the average metabolic rate was 83.8 kJ · d^{-1} (SD = 16.7), or 111% higher than premolt values (fig. 2). The corresponding figures for the redpolls were 26.8 kJ · d^{-1} (SD = 4.7) and 55.3 kJ · d^{-1} (SD = 10.7, 106%; fig. 3). The difference in metabolic rates between the five molt stages was tested with repeated-measures analysis for each species separately (bluethroats: $F_{4,20} = 30.83$, $P < 0.001$; redpolls: $F_{4,16} = 21.13$, $P < 0.001$). In addition, the analysis revealed that the patterns differed significantly between the species (species × stage: $F_{4,36} = 4.00$, $P < 0.01$). This was mainly dependent on redpolls' having relatively higher metabolic rates at PS 44–45. The postmolt metabolic rate was on average 15% higher than the premolt values in the bluethroats. In the redpolls, postmolt metabolic rates were 18% lower than the premolt values. However,

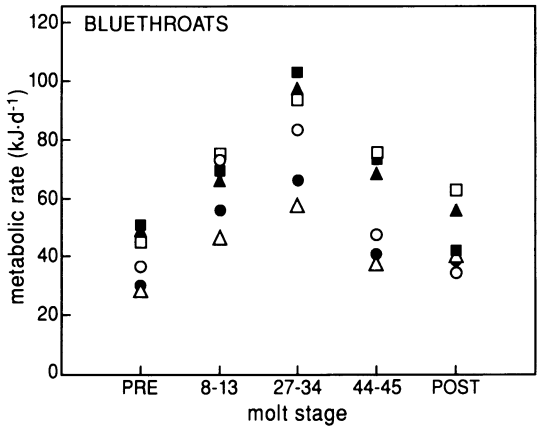

Fig. 2. Metabolic rates (kJ · d^{-1}) before, during, and after molt in six bluethroats, measured under thermoneutral conditions. Identical symbols refer to the same individual. Each bird was measured at primary scores of 8–13, 27–34, and 44–45.

neither of the differences was significant (bluethroats: $F_{1,5} = 2.33$, $P = 0.19$; redpolls: $F_{1,4} = 2.03$, $P = 0.23$).

The changes in m during molt in both species were at least partly explained by changes in fat scores. Further, we assume that a large part of the change is due to changes in water mass, which is correlated with feather growth intensity (Newton 1968; Evans 1969; Chilgren 1977; Chilgren and deGraw

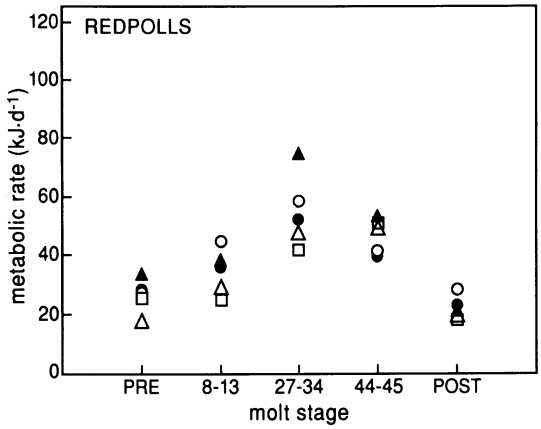

Fig. 3. Metabolic rates (kJ · d^{-1}) before, during, and after molt in five redpolls, measured under thermoneutral conditions. Identical symbols refer to the same individual. Each bird was measured at primary scores of 8–13, 27–34, and 44–45.

1977; Dolnik and Gavrilov 1979). Fat and water are nonmetabolic components and would influence our measurements only to a negligible degree. Also, since the mass changes follow the pattern found in the wild (for the redpoll; see also Evans 1966), the changes in metabolically active tissues can be considered to be a part of C_f. We have therefore refrained from correcting for changes in m during the progress of molt (see also Murphy and King 1984).

Overnight mass loss during the respirometry measurements was on average 2.4 ± 0.2 g (SD) before molt and 3.2 ± 0.4 g during peak molt for the bluethroats and 1.3 ± 0.1 g before molt and 2.2 ± 0.1 g during peak molt for the redpolls.

Cost of Feather Production

The significant variation in metabolic rate with stage of molt allowed us to estimate the cost of feather production (kJ · [g dry feathers]$^{-1}$). We did this by relating metabolic rate (in kJ · d^{-1}) to feather production rate (g dry feathers · d^{-1}) for each of the 11 individuals (fig. 4). As it is not obvious which of the nonmolting values (pre- and postmolt) should be used as a baseline value, we included both in our calculations. Slopes did not differ significantly between bluethroat individuals ($F_{5,18} = 1.25$, $P = 0.33$). The common slope was estimated as 836 ± 99 (SE) kJ · (g dry feathers)$^{-1}$ ($F_{1,23} = 75.5$, $r^2 = 0.83$, $P < 0.001$). In the redpoll also, slopes did not differ between individuals ($F_{4,15} = 2.0$, $P = 0.144$). The common slope was estimated as 683 ± 119 (SE) kJ · (g dry feathers)$^{-1}$ ($F_{1,19} = 32.8$, $r^2 = 0.66$, $P < 0.001$). The C_f did not differ between the species (ANCOVA, $F_{1,51} = 0.4$, $P = 0.51$). When we assumed an energy content of 22 kJ · (g dry feathers)$^{-1}$ (Murphy and King 1982), the efficiencies of producing feathers were 2.6% and 3.1% for bluethroats and redpolls, respectively.

Discussion

Feather production cost in the seed-eating redpoll was not significantly higher than in the insectivorous bluethroat, as would have been expected if the diet hypothesis were correct. We therefore conclude that differences in diet are not likely to explain the large differences in C_f that have been reported (Murphy and King 1991; Dietz et al. 1992).

Murphy and King (1990, 1991) suggested that the differences found in C_f between species may be related to the lengths of the nights during molt. According to this hypothesis we would expect molt costs to be inversely

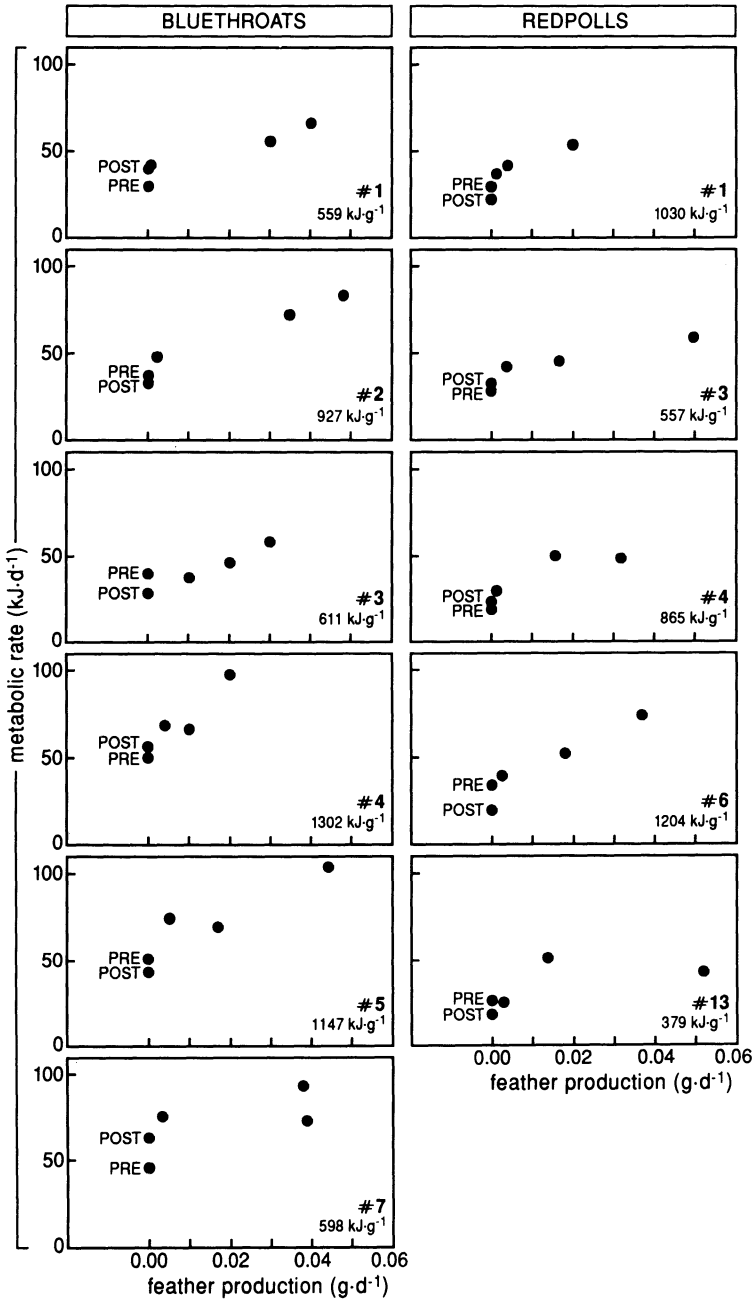

Fig. 4. Metabolic rates (kJ · d^{-1}) in relation to feather production rate (g dry feathers · d^{-1}) for individual bluethroats (six graphs on the left-hand side of the figure) and redpolls (five graphs on the right-hand side of the figure), as measured in thermoneutrality. The C_f (kJ · [g dry feathers]$^{-1}$) for each individual was calculated as the slope of the regression line of metabolic rate on feather production rate.

related to night length. Our results do not support this hypothesis. Both bluethroats and redpolls had even higher molt costs than most values reported before (Murphy and King 1991; Dietz et al. 1992), despite the fact that they molted under almost continuous daylight.

Instead, the fact that molt costs in bluethroats and redpolls were very high indicates that m may be an important factor to consider when exploring interspecific differences in molt costs. We surveyed the literature for data on C_f (table 2). Molt costs have been determined in two different ways, either from using indirect calorimetry or by measuring the ME. Values obtained from indirect calorimetry of molting birds in principle only reflect BMR and the additional heat production related to feather synthesis. In contrast, values obtained with the ME method normally also include the effects of locomotion, which may influence the final estimate of molt cost dramatically (as in our ME trials). As pointed out by King (1981), it is "clear that the measurement of ME as an estimate of moult costs is not adequate for all species or experimental designs."

Since only a few studies have been conducted on C_f, we chose to present them all (table 2; figs. 5, 6). We distinguished between values originating from the two different methods. For many of the ME-based values we had to obtain data on feather mass and m from sources other than the original study. This adds to the uncertainty this method involved. We therefore include in the statistical analysis only the seven species for which C_f was measured by indirect calorimetry.

The C_f (kJ · [g dry feathers]$^{-1}$) of the seven species was significantly correlated with m (kg) as

$$\log C_f = 1.984 - 0.382 \log m \quad (1)$$

($F_{1,5} = 10.0$, SE of the slope = 0.121, $r^2 = 0.67$, $P = 0.025$; fig. 5). However, if the costs of molt involve metabolic processes in addition to keratin synthesis (King 1981) and if these are proportional to m and require energy in proportion, molt cost should primarily be related to the mass-specific BMR, BMR_m (Dietz et al. 1992). The relationship between C_f and BMR_m (kJ · g^{-1} · d^{-1}) explains more of the observed variance in C_f:

$$\log C_f = 2.459 + 0.843 \log BMR_m \quad (2)$$

($F_{1,5} = 22.5$, SE of the slope = 0.178, $r^2 = 0.82$, $P = 0.005$; fig. 6).

In search of further evidence for a relationship between C_f and BMR_m, we calculated the residuals of log C_f from the regression on log BMR_m (resC_f; according to eq. [2]) and of log BMR_m on log m (resBMR_m; according

TABLE 2

Estimates of feather production cost (kJ · [g dry feathers]$^{-1}$) for different species of birds

	Body Mass (kg)	BMR (kJ/d)	Feather Mass (g)	Feather Production Cost (kJ/g)		Source
				$\dot{V}O_2$	ME	
Cardeulis flammea	.013	26.8	1.1	683		This study
Luscinia svecica	.017	39.7	1.2	836		This study
Fringilla coelebs	.020	33.5	1.4	230		Dolnik and Gavrilov 1979
Zonotrichia leucophrys	.025	40.5	1.7	488		Chilgren 1975 (cited in King [1981])
Falco tinnunculus	.210	77.8	20.1	106		Dietz et al. 1992
Asio otus	.280	106.0	31.6	90		Wijnandts 1984 (calculated in Dietz et al. [1992])
Anser anser	2.857	570.2	160.6	114		M. J. J. E. Loonen and R. van der Wal, unpublished manuscript
Carduelis flammea	.013	24.7	1.2		1,032	Dolnik 1965
Carduelis spinus	.014	25.1	1.3		478	Dolnik 1965
Carduelis carduelis	.017	30.1	1.5		1,225	Dolnik 1965

Carduelis cannabina	.017	29.3	1.5	1,009	Dolnik 1965
Emberiza schoeniclus	.018	26.0	1.6	471	Dolnik 1965
Fringilla coelebs	.020	33.5	1.4	397	Dolnik and Gavrilov 1979
F. coelebs	.021	32.2	1.9	743	Dolnik 1965
Fringilla montifringilla ..	.021	33.1	1.9	592	Dolnik 1965
Carpodacus erythrinus ...	.021	31.8	1.9	915	Dolnik 1965
Passer montanus	.022	34.0	1.5	495	Dolnik 1965
Emberiza hortulana	.022	36.0	2.0	445	Dolnik 1965
Zonotrichia leucophrys ...	.025	33.5	1.8	324	Murphy and King 1984
Passer domesticus	.026	41.0	1.8	473	Dolnik 1965
P. domesticus	.027	41.0	1.7	416	Blackmore 1969
P. domesticus	.027	40.2	2.0	835	Dolnik and Gavrilov 1975
Emberiza citrinella	.027	43.0	2.4	1,067	Dolnik 1965
Carduelis chloris	.029	41.1	2.6	612	Dolnik 1965
Pyrrhula pyrrhula	.030	47.7	2.7	311	Dolnik 1965
Coccothraustes coccothraustes	.048	60.3	4.3	123	Dolnik 1965
Falco tinnuculus	.210	77.8	20.1	117	Dietz et al. 1992

Note. The estimates are based on either indirect calorimetry technique ($\dot{V}O_2$, upper group) or measurements of ME (lower group). If data on body mass and BMR were not given in the original source, we used values presented by Gavrilov and Dolnik (1985). For nonoriginal BMR estimates we used values from summer and night as far as possible. When the amount of feathers produced was not given in the original source, feather mass was estimated from Turcek (1966). The value for *Asio otus* was calculated by Dietz et al. (1992). The value for *Anser anser* is based on the production of wing feathers only.

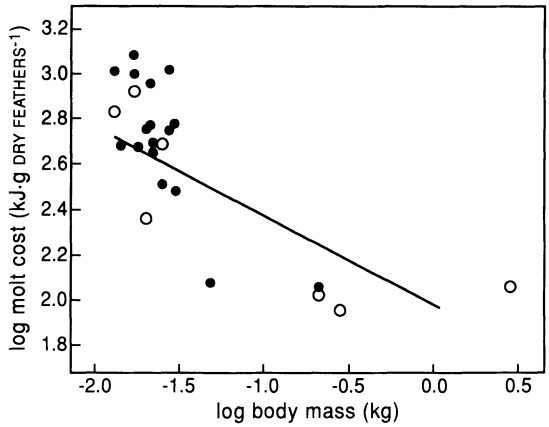

Fig. 5. Feather production cost (kJ · [g dry feathers]$^{-1}$) in relation to m *(kg) for different species of birds, as measured by indirect calorimetry ($\dot{V}O_2$, circles) and ME (dots). Values are from table 2. The ME values for* Fringilla coelebs *and* Passer domesticus *are the averages of those listed in table 2. The solid line is the best linear fit to the $\dot{V}O_2$ values.*

to the equation log $BMR_m = -0.602 - 0.489 \log W$ [in grams], $n = 7$). There was a significant correlation between resC_f and resBMR_m: resC_f = 1.92 resBMR_m + 0.0005 ($F_{1,5}$ = 10.7, SE of slope = 0.587, r^2 = 0.68, P = 0.022).

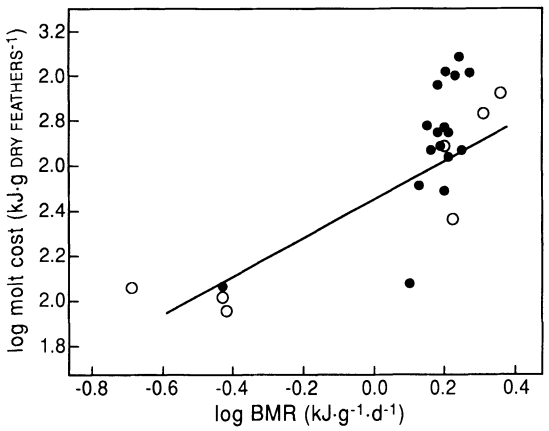

Fig. 6. Feather production cost (kJ · [g dry feathers]$^{-1}$) in relation to BMR_m (kJ · g^{-1} · d^{-1}) for different species of birds, as measured by indirect calorimetry ($\dot{V}O_2$, circles) and ME (dots). Values are from table 2. The ME values for Fringilla coelebs *and* Passer domesticus *are the averages of those listed in table 2. The solid line is the best linear fit to the $\dot{V}O_2$ values.*

This means that a species with a high mass-specific BMR for its mass also has, for its mass, a high C_f. It is thus clear that C_f is tightly linked to the BMR of a bird.

The coefficient (0.843) of log BMR_m in equation (2) is statistically indistinguishable from 1. This implies that the C_f is essentially proportional to BMR_m. In fact, the ratio BMR_m/C_f is independent of m ($F_{1,5} = 1.60$, $r^2 = 0.24$, $P = 0.26$) and is on average 0.0037 (g dry feathers) · (g body mass)$^{-1}$ · d^{-1} (SE = 0.00066, $n = 7$). Thus, C_f, for a species with known BMR_m, can be roughly estimated from the equation

$$C_f = 270\ BMR_m, \tag{3}$$

where C_f has the dimension kJ · (g dry feathers)$^{-1}$ and BMR_m has the dimension kJ · g^{-1} · d^{-1}. Consequently, the coefficient 270 has the dimension of d · (g body mass) · (g dry feathers)$^{-1}$. Accordingly, if we know the feather mass, the overall cost of molt (in kJ) can be estimated. If equation (3) holds for the whole size (or rather BMR) range of avian species, C_f will be predicted to vary from 26.6 kJ · (g dry feathers)$^{-1}$ for the ostrich *Struthio camelus* to 780 kJ · (g dry feathers)$^{-1}$ for the smallest passerines, for example, the goldcrest, *Regulus regulus,* for which BMR is known (Gavrilov and Dolnik 1985). With a general energy content of 22 kJ · (g dry feathers)$^{-1}$ (Murphy and King 1982), the efficiency of feather synthesis would vary over a range from 45.3% to 2.7%. In large birds this efficiency would be close to the biochemical efficiency of protein synthesis (40%–50%; Reeds 1991).

The tight association of C_f and BMR_m between species, together with the low efficiency values of feather synthesis, supports earlier suggestions that feather production costs include more than just costs for keratin synthesis: they consist mainly of costs of maintaining tissues necessary for feather production (King 1981; Murphy and King 1984, 1991, 1992; Dietz et al. 1992). It remains to be seen whether C_f also varies in proportion to BMR when BMR differs between and within individuals of a species.

Especially in small birds, the energy spent on feather synthesis may add significantly to the daily energy expenditure (DEE). For example, for a bluethroat that produces 1.2 g of feathers over 54 d, the cost of molt would on average add 47% to BMR throughout the molting period. As measured by us, this rise can be 111% during the most intensive part of molt, that is, the DEE is 2.1 · BMR because of feather growth and basal metabolic activities alone. It is clear that, with additional thermoregulatory costs of molting at low ambient temperatures, the overall costs of molt may severely impinge on other energetically expensive activities such as locomotion and fat deposition. For larger birds, though, that have a low production cost and carry

out the molt over a longer period of time (Ginn and Melville 1983), the additional costs of molt may have a relatively small impact on the DEE.

In conclusion, the C_f of birds is correlated with BMR, whereas neither diet nor latitude (night length) alone can explain the differences found between species. However, it should be noted that there are large discrepancies plaguing the available estimates of energetic costs of avian molt (table 2), and there is an obvious need for more controlled studies. Consequently, the possible importance of diet and feeding schedule in accounting for some of the intra- and interspecific variation in the costs of molt should not be dismissed. For a more detailed knowledge of the relationship between molt cost and BMR, further studies are needed on especially birds with low BMR_m.

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